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THE CLIMATIC CONTROL OF FLOWERING AND FRUIT SET[1]

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THE success of a plant species in nature largely depends upon its ability to reproduce, that is, to form ripe seed. Whereas potentially fruits can ripen the year round in tropical regions, in temperate climates fruits have to be ripe by the beginning of winter. This gives the plants a maximum period of about half a year to flower and produce fruit. In the large-fruited perennials where fruit growth takes almost that whole period, flowering has to be timed as early as possible without danger of frost damage. In the case of annual plants, a sufficient amount of vegetative development has to precede flower formation, to insure an adequate food supply to flowers and fruits. Thus in all these cases an accurate control of the onset of flowering is required, so as to synchronize fruit ripening with the yearly climatic cycle.

There are two major climatic factors, which vary with the seasons, and which can be employed for synchronization purposes. These are (1) length of daily light period, and (2) temperature. Of these two the former is the most accurate; in fact, it is the factor upon which we base our human time reckoning. In the first paper of this symposium we have heard how photoperiod controls, not only flower initi-

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ation, but also further flower and fruit development in a large number of plants. Based upon the preceding considerations of the requirements for fruit ripening, we can divide the plants of temperate regions into the following groups as to their photoperiodic response:

(a) Annuals are in general short-day plants, which gives them an opportunity to delay flowering until the last safe moment.

(b) Annuals from the California deserts, where ripening of the fruits has to be completed by May, because of the summer drought, are almost exclusively long-day plants.

(c) Biennials and perennials are usually long-day plants. They can start flowering on the reserves laid down in the previous year and thus have a long period for fruit ripening.

In the last thirty years we have obtained a fairly satisfactory understanding of the extent to which photoperiodism controls plant development. This is partly due to the vigorous attack of this problem by research workers largely in the U.S.A., but also to the relative simplicity of experimental work with photoperiod, which can easily be controlled by shading or by providing supplemental light. If we want to study the effects of temperature on the development of plants, we need much more elaborate experimental facilities. These are available in only a few research centers, which explains why so much less is known about temperature effects on plants than about photoperiod. Because of this discrepancy in knowledge we probably have a wrong conception about the relative importance of photoperiod and temperature in the development of plants.

There are two major temperature cycles in nature: a yearly and a daily. Let us first consider the relationship between the yearly temperature cycle and plant life. Active growth requires in general a fairly high temperature which usually does not occur during winter. The low winter temperatures, however, do not just retard growth, but they also control and synchronize plant development along two different lines. In the first place low temperatures can act as a sort of trigger. This was first clearly described by Frederick Coville in 1920. He pointed out that the break-

ing of dormancy of buds of deciduous plants is dependent upon a sufficient exposure to cold during winter. It is amazing that our present knowledge hardly extends beyond Coville's statements. Buds of deciduous plants are formed in spring or early summer, and in the course of the summer pass into a state of dormancy, which prevents them from developing when they are brought under favorable conditions. When these deciduous plants are kept in a greenhouse at favorable growing temperatures, their buds remain dormant, and they can be kept indefinitely in an inactive state, by keeping them in the greenhouse. Their dormancy can be broken at any time by placing them for one or more months at low temperatures (near freezing). We know nothing about the quantitative aspects of this temperature effect; it is generally conceded that only temperatures below 10° C., more particularly between 0° and 5°, are effective. It is also known that deciduous trees from colder climates have a longer chilling requirement than trees from warmer climates. Thus in Southern California peach varieties from the Midwest can not grow, because the winters are too mild and do not provide sufficient cold to break dormancy. On the other hand, peach varieties, such as the Babcock, which do well in Southern California, are killed in more northerly regions, because their chilling requirements are met too early in winter. Thus they are liable to come into leaf long before the danger of frost is over, and are killed consequently. Not only trees, but also other plants have such a need of cold shock to bring them out of dormancy, keeping their development synchronized with the seasons. A typical example is the lily of the valley, *Convallaria*. Its corms can be brought into growth any time by placing them for a few weeks at 0° C. Flowering of biennial plants like beets or henbane is equally brought on by cold treatment. We must concede then that cold shock is an important and widespread mechanism of coordinating plant growth with seasons.

A variant of this mechanism is vernalization, in which a period of chilling very early in the life of the seedling regulates its subsequent development.

There exists another type of temperature response which

is capable of synchronizing plant development with the yearly seasonal cycle. This is based on differential optimal temperatures of the various physiological processes which succeed each other in normal development. This response has been worked out in great detail by Blaauw and collaborators, and is particularly well developed in most bulbs. The growing point of a tulip, for instance, goes through a cycle of developmental processes which takes about one year. This cycle can be speeded up to at most seven months, or it can be retarded to two years. In nature it keeps to an accurate twelve-month cycle. This is due to the fact that each stage in the cyclic development of the growing point has a different optimal temperature and that these optima differ so much, that no single temperature, if

TABLE 1

Data from Blaauw and Collaborators on Optimal Temperatures (in Degree Centigrade) for Organ Formation and Stem and Root Elongation in Several Bulbous Plants

	Initiation		Preparation for Stem Elongation	Actual Stem Elongation	Root Development
	Leaf	Flower			
Hyacinth	34	25	13	22	27
Tulip	20	20	8–9	13–23	
Bulbous Iris	13	7–9	15	15	

maintained constantly, could satisfy the whole developmental cycle. First leaf initiation and flower initiation require an optimal temperature of 25° C., and neither at 5° nor above 30° can flowers be initiated. The next stage lasts fairly long; during these two months a low temperature of 8–9° has to prevail if normal elongation of the stem is to occur afterwards. The processes preparing the growing point for elongation do not proceed at 20° or higher. Finally the actual stem elongation goes on best at 13–17°. In the hyacinth and bulbous iris the actual optimal temperatures for the various stages of development differ somewhat from the tulip, as shown in the table, but they have in common that high optimal temperatures, which they receive during summer, are followed by low optimal temperatures. The processes requiring the low temperatures are thus delayed

until late fall, and actual elongation does not start until temperatures are rising again in spring. Any deviation from this cycle results in serious upsets in development, and if the temperature deviations are large enough, as is the case when bulbs are grown in the constant temperatures of the tropics, all further development of the bulbs is suspended and they die within a year.

A similar temperature cycle was found by J. Bonner in the Camellia. In this plant flower initiation and flower bud growth require high temperatures, such as occur during summer in the warmer regions. The final stages of flower bud growth and flower opening on the other hand require cool weather with nights at or below 10° C. Therefore warm summers have to be followed by cool winters if Camellia is to be grown successfully.

Thus far we have dealt with temperature-controlled mechanisms in the development of plants, which each require weeks or months for their completion. There are also temperature cycles which can be measured in hours. They are connected with the daily temperature cycle. During day and night entirely different physiological processes occur in plants. Carbon dioxide reduction and other photosynthetic processes proceed only during day, and in general have high optimal temperatures. As was known for a long time, in many plants actual growth occurs predominantly during night, and the optimal temperature for growth turned out to be considerably lower than for photosynthetic processes. As pointed out by Parker, the reaction which controls the photoperiodic response is also a dark reaction proceeding during night.

Thus we see that in conjunction with photoperiodism there exists in plants also thermoperiodicity. In any general considerations this thermoperiodicity can not be separated from photoperiodism, because both of them are based on the daily light cycle. Actually, before the existence of thermoperiodicity was clearly pointed out, it was known that temperature was of primary importance in the expression of photoperiodism. But also in plants which are indeterminate as far as daylength is concerned we encounter thermoperiodicity.

To study thermoperiodicity, greenhouses and laboratories must be available in which temperature can be controlled within narrow limits, even under full sun radiation load. This had not been accomplished until very recently. Now the air-conditioned greenhouses and the artificial light rooms with controlled temperature and humidity of the Earhart Plant Research Laboratory of the California Institute of Technology in Pasadena provide ideal conditions for a study of the temperature responses of plants. By passing a sufficient amount of air past plants in the greenhouses and by insuring an even distribution of the air stream, local heating effects of the incident radiation can be prevented. The low specific heat of air makes it necessary to use large volumes of air to lower the temperature of surfaces heated by the sun's radiation. It was really the solution of the problems connected with the circulation of such large volumes of air without creating localized air streams of undesirable velocities, that made the construction of the new air-conditioned greenhouses a success.

All plants in the Earhart Laboratory are grown on wheeled steel tables, and are moved daily from condition to condition. In this way the effects of a large number of combination-treatments can be investigated. For instance, plants receiving all the same treatment during day, by growing them together in one greenhouse, can be subjected to a variety of conditions during night. Or plants, kept under one night condition, can be subjected to many different temperatures and light intensities during day.

As a typical example of thermoperiodicity work in the Earhart Laboratory on the tomato plant (var. Essex Wonder) can be cited. When grown in full daylight in a greenhouse at 20° C. for eight hours daily, optimal growth was obtained (expressed as wet weight at the end of three months' treatment) when kept at 10° during night. In a 28° greenhouse the heaviest plants were found at 17° night temperature. In a more complete experiment plants were grown in different temperatures (4, 6, 10, 14, 17, 20, 23, 26 and 30° C.) either in light of about 1,500 fc. for eight hours daily or during the dark period of sixteen hours. Seventy days after the beginning of the differential treatment there

were large differences in size and weight between the treatments. At all levels of night temperature there was a typical optimal rate of growth and greatest weight at some intermediate day temperature, and something similar was true for the different day temperature levels. Yet in all cases the plants had received an identical amount of light. This shows that at that light level (1,500 fc.) growth is not limited by light but by temperature-controlled processes, which differ from day to night. By comparing plants which received the same total daily heat sums (expressed as the sums of the degree centigrade for each of the 24 hours), the following figures were obtained. At 300 degree-hours optimal day- and night-temperatures were 17° and 10°, at 400 degree-hours these optima were 19° and 15.5° and for 500 degree-hours they were 21° and 20.5°. Thus in each case cited above the optimal day temperature was higher than the optimal night temperature. This is probably not true any more at day temperatures of 10° and lower. It also is not true of the optimal temperatures for fruit set. In that case day temperature is relatively unimportant, but fruit set and fruit development is almost exclusively controlled by the night temperature, with only a minor modifying effect of day temperature. On the other hand, age of the plant is of major importance in the optimal temperature for fruit set. During the first period that any fruits are set, the optimum lies at 21 or 22° C. depending on whether the day temperature was 28 or 20°. During the next half month these optima were 18 and 20°, and another 20 days later these values had shifted to 14 and 14°. This same phenomenon occurs in other plants, such as in the chili pepper.

All these facts have important ecological implications. In the first place, it is of interest to note that the normal fluctuation in daily temperatures has a close counterpart in a daily shift in optimal growing conditions for plants. It really seems as if the adaptation of plants to their surroundings has gone to the most extreme ends, in that, just like in the yearly temperature cycle, plants are adapted to follow the naturally occurring daily temperature cycle of nature. In the second place we find that as the season

progresses and the day and night temperatures are gradually decreasing from their mid-summer maxima, the optimal temperatures for fruit set are also decreasing, closely following the naturally occurring conditions.

In other plants we encounter very different temperature responses. The African violet, *Saintpaulia*, grows best at low light intensities, and warm day and night temperatures (as high as 26° C.). This closely approaches the climate in a tropical forest, where the African violet is native.

Spring- and early-summer-flowering plants are usually low-temperature plants, such as stocks and English daisies. Neither of these flowers when the day or night temperatures are high, but in the English daisy a very low night temperature may partly offset a higher day temperature, which is not the case in the stock. In the stock plants vegetative growth is possible over the whole temperature range tried, but initiation of flowers is completely dependent upon day temperatures below 20° and night temperatures below 18°. In summer-flowering plants we may find the reverse: at the lower night temperatures no flowers are formed, as in petunia. Thus we see that thermoperiodicity is an important factor in the flowering and fruiting behavior of plants and also tends to synchronize plants and seasons.

There are all sorts of interactions between photoperiodism and thermoperiodicity. Since we know so little about it as yet this will not be discussed, but only mentioned. It allows for a rather amazing degree of control of flowering. A thorough understanding of all these interacting influences is necessary for a complete explanation of the climatic behavior of plants.

In a few cases it is known already that the photoperiodic behavior of plants is under genetic control. The same thing is undoubtedly true for thermoperiodicity. The responses of plants to their surroundings are the characters for which plant breeders are selecting, but this can not be done deliberately until this behavior has been analyzed physiologically. The temperature response must be fairly complex, but once all genes involved are known, a directed breeding program can be undertaken. At present selection is mainly on the basis of yield, but there are so many inde-

pendent factors influencing yield, such as the photosynthetic mechanism, water economy, temperature tolerance, root development, photoperiodism, etc., that many desirable characters are likely to be lost in a general breeding program aimed at yield.

The temperature responses discussed in the previous paragraphs make it clear why it is impossible to use average yearly or daily temperatures, as published by the weather bureau, to predict what plants will do well in which climate. An average daily temperature of 25° may be made up as 25° during day and 25° during night, which would give good growth and flowering of African violets, good growth and flowering, but no fruit set in tomatoes, good growth but no flowering in stocks and no growth at all in English daisies. When the same average temperatures were distributed as 35° during day and 15° during night, African violets would do poorly, but tomatoes would set fruit. To predict the fruiting behavior of tomatoes it is necessary to know the night temperatures in a given locality. For the flowering of stocks it is necessary to know both the average night temperature and the maximal day temperature. For predicting the success of bulb culture, the average monthly temperatures are needed. This shows that we need accurate knowledge of temperature response of plants, and detailed meteorological information of a different type than what is usually available, before climate and plant growth can be correlated in terms of a physiological ecology. Such information would be highly useful in the settlement of new areas, and in the selection of the most logical crops for any area in the world.

More detailed information about the climatic control of plant growth will have other applications as well. We might summarize these under the general term of weather control. The most obvious of these is the technological change of weather conditions, such as exerted in greenhouses, lathhouses or with the aid of orchard heaters or cheesecloth covering. Certain extensions or refinements of these procedures are possible, as soon as we know what we have to achieve. Since we are gradually led to the conclusion that control of the night condition is most important

in the growing of so many plants we may be able to devise controls which will be effective during night only (as an example photoperiodic treatments with extra light of low intensity during night can be mentioned).

A second method of weather control lies in changing the period of sowing of annual plants. Since each "climate" is really a succession of periods with more or less light and higher and lower temperatures, it often is possible to subject plants to the proper conditions at their critical periods by delaying or advancing development. Here the use of growth-regulating substances may become of great importance.

A third method of weather control lies in the development of long-range weather forecasting. This is at present in its infancy. It would seem that, if weather forecasts a few days ahead are possible, there are no logical reasons why the same thing can not be done for longer periods. If for instance in the beginning of May it can be predicted whether the night temperatures in July will be higher or lower than usual, a tomato variety can be selected and planted which will do best under the expected weather conditions, and will set best. This is very important, because the temperature range within which most tomato varieties produce commercially profitable amounts of fruit is surprisingly narrow, and one or two degrees difference in night temperature may mean production of only half or one third of the possible maximal production.

All these considerations show that in the future we can look forward to an era when improved knowledge about weather responses of plants will make it possible to remove a number of the climatic hazards which now beset the farmer. Then agriculture will have progressed from an art to a technology, and the old saying of Mark Twain, that every one talks about the weather, but nobody does anything about it, will become a historical curiosum. The importance of these new developments looms so large in my mind that I am willing to predict that the second half of the 20th century will go down in history as the Agricultural Revolution.

GENETICS OF FEATHER PIGMENTATION IN THE FOWL

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A WIDELY accepted hypothesis attributes control of feather pigmentation in the fowl to a pair of autosomal genes designated as *C* (chromogen) and *O* (oxidase). Since these assumptions are fundamental to interpretation of all plumage patterns, they warrant close scrutiny. The hypothesis deems precursor-substance and an enzyme-system necessary to melanin formation (Jull, 1940). Accepting this premise as valid, two possibilities arise in respect to origin of recessive white plumage: (1) chromogen or oxidase may be absent in all somatic cells, or (2) chromogen or oxidase may be absent only in feather germs. Absence of both components is theoretically possible, but the two known forms of recessive white are complementary, producing F_1 colored progeny, thus suggesting the genotypes (*c c O O*) and (*C C o o*).

Occurrence of melanic iris and dermal pigment in fowls with recessive white plumage, *e.g.,* Jersey White Giant and White Silkie, excludes the first alternative and narrows consideration to one or more components of the feather germ. The immediate issue then becomes precise location of pigment-forming potential.

Evidence provided by histological, embryonic transplant, and *in vitro* explant studies confirms the view that feather pigment is elaborated exclusively by melanocytes of neural crest origin (Post, 1894; Rawles, 1948; Strong, 1902). Keratinoblasts of the feather germ accept and deposit preformed melanin granules, but are themselves incapable of synthesizing pigment. Precursor-substance and an enzyme-system are reactants within cell bodies of melanocytes. Wherefore, the chromogen-oxidase hypothesis must stand

or fall on the basis of evidence afforded by melanocyte behavior in feather germs of white plumage.

Melanocytes are present in feather germs of embryos and adults of white varieties, and have been cultured in explants of embryonic skin (Hamilton, 1940). Pigment granules in small numbers are invariably present in feathers of white plumage (Bohren, Conrad and Warren, 1943). Gray or black-splashed defect-feathers are not uncommon in recessive white plumage; and exceptional black feathers also occur. The writer demonstrated melanocytes in feather germs of 3- and 4-year-old Jersey White Giant hens by the method of Lillie and Juhn (1932). Clearly, functional agents for elaboration of melanin exist, and melanoblast reserves persist indefinitely in feather germs of recessive white plumage. Reference of recessive white to absence of chromogen or oxidase in such melanocytes poses a biochemical absurdity.

Present inquiry is not concerned with the mechanism of melanin formation, but solely with its persistence in fowls with white plumage. One aspect of the chromogen-oxidase concept deserves brief consideration, however, because of relevance to fundamental metabolism. Melanin may be formed from a diversity of phenol and polyphenol derivatives. Such compounds are so widely distributed in plant and animal organisms that it becomes a practical impossibility to designate an instance in which "melanogen" is indubitably absent. Limiting consideration in the fowl to amino-acids such as dispensable tyrosine, and indispensable cyclic members of the chromogen group (phenylalanine and tryptophane), it would seem that a non-chromogen status connotes a deficiency incompatible with cellular life. Still further, it has not been demonstrated that feather melanin is elaborated from a single substrate. Hence, multiplicity of sources from which melanin may be directly or indirectly derived renders assumption of "melanogen" control by a single gene extremely dubious.

An essentially unlimited supply of melanogen is always present in viable fowls. This circumstance has special bear-

ing upon behavior of melanocytes in explants and in feather germs. Transition from the melanoblast to the melanocyte stage is marked by inception of pigment-granule formation. Unless opportunity to discharge pigment prevails for the melanocyte, granules accumulate to obscure all cell structure save the nucleus; protoplasmic cell processes are retracted; the melanocyte undergoes sphering and degeneration, as in the case of other free metazoan cells subjected to deleterious accumulation of metabolites. Melanocytes are positively thigmotactic in relation to living membranes and non-living surfaces, *i.e.*, feather germ epithelium in the organism, and cover-slips in explant preparations. Where normal discharge of pigment (by pinching off bulbous, granule-laden tips of cytoplasmic processes in contact with receptive keratinoblasts) is precluded, the melanocyte literally destroys itself by unbridled melanin formation. Significantly, the latter reaction is manifested by melanocytes of feather germs in white plumage, even in the most actively proliferating collar segment.

Melanocytes of feather germs in colored breeds orient themselves in contact with palisades of keratinoblasts engaged in barb and barbule development. Here, they thrive in large numbers. It is in the upper levels of the feather germ, where transition from keratinoblast to keratinocyte renders the latter non-receptive to pigment, that melanocytes exhibit sphering and degeneration.

Hamilton (1940) suggests that observed differences in melanocyte viability account for the origin of white plumage, *i.e.*, melanocytes of white varieties degenerate before transfer of melanin to keratinoblasts can be accomplished. Apart from the fact that a simple qualitative difference fails to explain mode of inheritance and segregation ratios in mating experiments, it would seem that impaired viability and non-persistence of melanocytes in white feather germs represent concomitant effect, rather than efficient cause of whiteness. Thus, factors preventing (1) discharge of pigment by melanocytes, and (2) acceptance of pigment by keratinoblasts would have a common

deleterious effect upon melanocytes. Wherefore, white plumage may arise in consequence of extrinsic factors, as well as of intrinsic deficiencies, with respect to melanocyte metabolism, viability, and persistence.

Feather pigmentation depends upon coordinative unity of three components: (1) thigmotactic orientation of melanocytes in relation to keratinoblasts, (2) transfer of preformed melanin from melanocytes to keratinoblasts, and (3) acceptance of discharged melanin by keratinoblasts. It is apparent from the facts of feather development that critical periods exist, prior or subsequent to which pigmentation of feather substance is precluded. Disturbance of adjustment, as regards temporal or material factors, would interfere in variable qualitative and quantitative fashion with the process of pigmentation. It follows that the origin of white plumage may be sought within the province of the mechanisms indicated. Obviously, the sphere of melanogen and enzyme-system reactants is of collateral importance, but once established, becomes extraneous to the immediate issue of pigment transfer and acceptance. Consequently, it is submitted that the chromogen-oxidase hypothesis not only fails to reflect the actual state of affairs prevailing in feather germs of white varieties, but also has no standing as a first approximation with reference to the pigmentation process as such.

The foregoing suggests an inherent defect of the chromogen-oxidase hypothesis which may, however, be easily overlooked: the chromogen-oxidase hypothesis interprets feather pigmentation in terms of biochemical properties, rather than as an operational process in an immediate sense. Biological concepts are equally susceptible with physical theory to adverse criticism on that score (Bridgman, 1936).

An hypothesis is offered to meet the situation, consistent with pertinent and relevant morphological, physiological, and genetic data. It is suggested that pigment formation by melanocytes is "excretory" in respect to the producer-cell, and "secretory" as regards the recipient-cell. Acceptance or non-acceptance of melanin by keratinoblasts may

be akin to variation of opsonic potential in leucocytes. Whatever the ultimate chemical physics involved, genetic control of feather pigment is referred to an operational process, and a pair of autosomal genes regulating component phases: (1) pigment transfer by melanocytes, and (2) pigment acceptance by keratinoblasts.

Gene *Tr* is associated with expression of the transfer mechanism whereby melanocytes discharge preformed melanin granules; the recessive allele *tr* coincides with non-expression of the transfer function, resulting in complete,

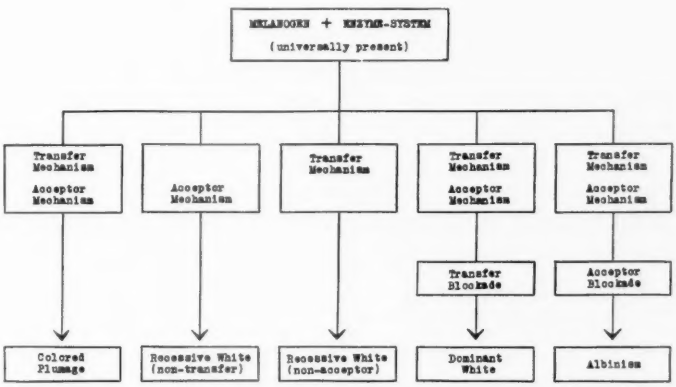

FIG. 1.

or almost complete, failure of pigment delivery in the normal manner.

Gene *Ac* is associated with expression of the acceptor mechanism whereby keratinoblasts phagocyte and deposit melanin granules; the recessive allele *ac* coincides with non-expression of the acceptor function, resulting in complete, or almost complete, failure of pigment ingestion in the normal manner.

The common recessive white genotype, as in White Minorca, White Plymouth Rock, and White Wyandotte, is conceived to be (*tr tr Ac Ac*), and is designated the *non-transfer* form. Recessive white as in Silkies reported by

Bateson and Punnett (1906) is assigned the genotype (*Tr Tr ac ac*), and is designated the *non-acceptor* form.

Dominant white, as in the White Leghorn, is attributed to the influence of gene *I* blockading the transfer mechanism of melanocytes. Presence of melanocytes in albinotic vertebrates, as well as "ghost patterns" in such forms, suggests that the condition is not due to absence of melanogen or enzyme-system in the pigment-forming cells. Autosomal and sex-linked albinism in the fowl are correlated with recessive alleles at pigment loci, factors conceived as blockading the acceptor mechanism for melanin and allied pigment in all somatic areas.

Processes concerned in blockading transfer or acceptor mechanisms are interpreted as intracellular phenomena. Moreover, the nature of these processes appears to be that of surface reactions, *i.e.*, interference with passage of pigment particles through the ectoplasmic layer and cell membrane. The preceding concept is in accord with observed reactivity, and excludes intervention of extracellular, diffusible, enzyme-like substances. This would account for absence of suppressor effects in tissue extracts, *e.g.*, lack of inhibitor-substance in White Leghorn embryo filtrate, and absence of the same in ectodermal explants. Results of ectodermal, mesodermal, and wing-bud transplants, as well as observations on feather pattern at margins of skin transplants in day-old chicks, are also in harmony with the view expressed, and opposed to extracellular diffusion of enzyme-like inhibitor-substance. The intracellular processes may be endo-enzymatic in the same sense that polarization phenomena are induced. This would be in conformity with available data on cellular behavior incident to the pigmentation process. It is for these reasons that the reactions are designated as blockade phenomena, distinguishing them from effects of hypothetical, extracellular, diffusible inhibitors.

Non-transfer recessive white $\times$ non-acceptor recessive white produces F_1 colored progeny, and an F_2 ratio of 9 colored : 7 white (Bateson and Punnett, 1906). A cross

involving dominant white, and either type of recessive white, produces white F_1 progeny, and an F_2 ratio of 13 white : 3 colored (Snyder's dominant and recessive epistasis). The mating colored × recessive white, and its reciprocal, produces F_1 colored progeny, and an F_2 ratio of 3 colored : 1 white. Dominant white × colored, and its reciprocal, produces F_1 white (or color-ticked white) progeny, and an F_2 ratio of 3 white : 1 colored. Extracted dominant white from White Leghorn × Jersey White Giant, carrying the genotype (*tr tr Ac Ac I I*), crossed with non-transfer white (*tr tr Ac Ac i i*), produces F_1 white progeny, and an all-white F_2 generation.

Differential behavior of eumelanocytes and pheomelanocytes will not be broached at this time, but it is submitted that interpretation of pattern mechanisms (*e.g.*, occurrence of the pyle pattern on a background of recessive white, dominant white, or color) is facilitated by the transfer-acceptor hypothesis, or flexible modifications of the same which do no violence to credulity. Above all, however, hitherto paradoxical occurrence of functional melanocytes in feather germs of fowls with white plumage becomes understandable by adopting the transfer-acceptor hypothesis. Concordance of morphological, physiological, and genetic observations with expectancy in all instances renders the transfer-acceptor hypothesis entirely plausible.

Summary

Evidence is marshalled to show that the chromogen-oxidase hypothesis of feather pigmentation in the fowl is untenable. An alternative concept, based upon the cellular physiology of melanocytes and keratinoblasts, is proposed. Feather pigmentation is attributed to concurrence of transfer by melanocytes, and acceptance by keratinoblasts of melanic pigment. A pair of autosomal genes, *Tr* and *Ac*, controls the mechanism of feather pigmentation. The recessive allele of either gene in homozygous form coincides with recessive white plumage. Dominant white is conceived as blockade of the transfer mechanism at cell sur-

faces of melanocytes. Albinism finds explanation in blockade of the acceptor mechanism at surfaces of pigment-receiving cells in all somatic areas. Data of breeding experiments are in accord with results anticipated by the transfer-acceptor hypothesis.

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FURTHER STUDIES OF AUTOSOMAL NAKEDNESS IN THE DOMESTIC FOWL[1]

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IN a report and description of a new type of autosomal dominant nakedness in the fowl, Sturkie (1942) showed that the character varied in expression from an extreme degree of nudity to an almost normal condition. The mortality for the first 15 days of life was very high. This study covered only two generations of transmission of the character, and the possible effects of modifiers against the degree of nakedness and the high degree of lethality associated with the character were studied. It was found, however, in this short period that modifiers had not accumulated against the character.

The present report concerns the study of the character and its behavior through eight generations of natural selection.

Naked males (heterozygotes) were selected each year and mated to normal White Leghorn females. No attempt was made to select males from families showing the least mortality, or males from families exhibiting any one degree of nakedness. The males selected were usually of intermediate grade (Grade III), and these were selected without regard to pedigree or family record. The chicks were classified with respect to nakedness into four main groups or classes. Grade IV chicks exhibited the most extreme degree of nakedness and Group I the least. Mortality records were kept for the first 15 and 30 days of life except for the fourth generation. The naked chicks were brooded at a slightly higher temperature than were normal chicks.

[1] Paper of the Journal Series, New Jersey Agricultural Experiment Station, Rutgers University–The State University of New Jersey, Department of Poultry Husbandry.

Results

Effects of natural selection on degree of nakedness: The frequencies of the grades of nakedness by generations are shown in Table 1. In general, for the first three generations, the frequencies of the more extreme grades of nakedness are higher, but in the succeeding generations, particularly in the seventh and eighth, the lower grades are more frequent.

TABLE 1

FREQUENCIES OF GRADES OF NAKEDNESS BY GENERATIONS

No.; Grade & Generation of Naked Sires	No. of Progeny	Grade Frequencies in Percent. I	II	III	IV
A-III-1	395	9.8	41.6	37.6	11.0
B-III-2	118	5.0	19.5	26.3	49.2
C-III-2	112	9.1	25.8	25.0	40.1
D-II-2	92	10.5	18.4	38.5	32.6
E-I-2	176	63.6	23.8	9.8	2.8
F-3	71	8.45	23.94	39.43	28.17
G-3	68	4.41	30.88	26.47	23.53
H-I-4	72	70.83	12.50	11.11	5.55
I-III-4	30	30.00	3.33	13.33	53.33
*J-III-5	179	44.13	17.87	18.43	19.55
K-IV-5	88	50	21.59	13.63	14.77
L-III-6	216	36.57	33.33	18.51	11.57
M-III-7	83	56.6	27.7	15.7	0.00
N-III-8	28	60.7	21.4	14.0	3.5

* Homozygous for nakedness. All other males heterozygous.

Progeny of two of the Grade I males (E and H, generations 2 and 4) also showed a higher incidence of Grade I.

Mortality: The mortality for the naked chicks by generations (except the fourth) is shown in Table 2. In the third generation the mortality dropped to about half that in the first and second generations, and then declined thereafter through the seventh generation to a low of 6 per cent.

TABLE 2

MORTALITY OF NAKED CHICKS BY GENERATIONS

Generation	Total No. of Chicks Hatched	Percent. Dead at 15 days of age	30 days
1 & 2	221	57.9	64.2
3	184	27.1	33.7
5	228	26.75	-
6	216	20.83	21.29
7	83	6.00	6.00
8	28	9.00	9.00

In the eighth generation the mortality was 9 per cent., but the numbers were small, and this probably does not represent an increase over the previous year.

In the earlier study (Sturkie, 1942) it was shown that the naked chicks during the first two generations consumed less feed than normal chicks, and the mortality could be decreased about one half by increasing feed consumption through the feeding of wet mash. In later generations feed consumption was not measured, but the decrease in mortality occurring in the third and later generations may be due in part to greater feed consumption. Since the heat loss in the naked chicks is higher than for normal chicks, it was thought that the degree of nakedness might figure significantly in the mortality. Thus, the mortality in rela-

TABLE 3

MORTALITY AS RELATED TO DEGREE OF NAKEDNESS. PROGENY OF NAKED MALES (HETEROZYGOTES) × WHITE LEGHORN FEMALES.

Generation		Grades of Nakedness I	II	III	IV
1 & 2	Number hatched	92.0	130.0	65.0	33.0
(av.)	Percent. dead*	67.4	65.4	70.7	42.4
3	Number hatched	16.0	30.0	35.0	45.0
	Percent. dead	56.2	33.3	34.3	22.2
5	Number hatched	108.0	43.0	36.0	41.0
	Percent. dead	18.51	23.25	30.6	48.8
6	Number hatched	79.0	72.0	40.0	25.0
	Percent. dead	13.92	19.44	27.5	40.0

*Naked chicks dead at 15 days.

tion to degree of nakedness was studied (Table 3). It is observed that for the first three generations mortality was not related to degree of nakedness, since the mortality in the chicks exhibiting the less severe grades of nudity was as high as or higher than those of the more extreme degrees. In generations five and six the mortality was somewhat higher for the chicks with the least feathers.

As mortality in generations seven and eight was low and the numbers of chicks were small, it was not possible to study this relationship.

These results suggest that the heat loss in later generations was greater for the more naked birds. This may have been due to less attention to brooding conditions than in the case of the first three generations of chicks, where apparently heat loss was not a factor, since the mortality was not related to degree of nakedness.

Discussion and Summary

The results of this study show that genetic modifiers against nakedness and the high mortality associated with it have accumulated as a result of natural selection over a period of eight generations and support Fisher's (1935) theory of dominance in poultry. The greatest drop in mortality as a result of selection occurred in the third generation, whereas the relative increase in number of chicks with more feathers occurred in the fifth and sixth generations.

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THE RISE AND FALL OF THE WHITE GRUB IN PUERTO RICO

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THE extensive masonry aqueducts on the south coast of Puerto Rico, so well constructed of brick and stone that many of them are still in use, but so ancient that no one alive can tell when they were built, are conclusive evidence of the early establishment of the means of irrigation for the growing of sugar-cane in this part of the island. In the many years when the value of the coffee crop equalled or exceeded that of sugar, these lands were always in cane, for there was no other crop to which they were so well adapted. Yet in the early accounts of the insects attacking sugar-cane, only incidental mention is made of white grubs, which subsequently had become the major pest of every crop by the time of the American occupation. Reconstruction of the cane-field environment at that time should indicate what former factor or factors in natural control had been minimized or eliminated to make possible such an enormous increase in the numbers of white grubs.

This is not so difficult as might be expected, for a mysterious disease of sugar-cane, thought by Mr. José I. Otero to be dry top-rot, first appearing in the region south of Mayagüez in 1870, soon spread extensively in the western and southwestern portion of the island. That eminent naturalist, Dr. Augustín Stahl, fully as much interested in all aspects of natural history, even economic, as in his patients, in his extensive study of the disease (1880), wrote:

> Under the cane plants and between their roots one may find the larvae or the perfect stages of the rhinoceros beetle ("gran cigarrón"), *Strataegus Titanus;* of the "black hard-back" or the "brown hard-back" ("cáculo

negro y colorado"), *Ligyrus chalcpus* and *Ancylonycha;* various little cockroaches or orthoptera; a very small beetle which perforates the sick or dead rootlets; ants, and other species of little insects even less known; but all of these little animals are attracted by vegetable material dead or in a stage of decomposition, without causing any damage to sound roots. . . .

In this statement he is quite correct in anticipating the rearing experiments of later entomologists as to the role of *Ligyrus* beetle grubs: partially so as to the grubs and adults of the rhinoceros beetle; but quite incorrect as to the grubs and adults of the common white grub, identified by him as *Ancylonycha,* which feed only on living vegetation. He was quite sure of his position, however, and in a later publication (1894) states that:

The illustrious Agronomic Engineer, Director of the Agricultural Station at Rio Piedras, Don Fernando López Tuero, is of the opinion that the *cause* of the disease of sugar-cane . . . is the larva of a scarabaeid beetle called "gusano blanco ó palo viejo," of which the adult is called "cáculo." . . . "Cáculo" is a corruption of "cálculo" or little stone ("piedrecita") to which these insects are similar. Two distinct genera are known, the black beetle and the red or yellow: the black beetle is *Ligyrus chalepus,* and the yellow belongs to the genus *Ancylonycha,* both belong to the family of the Dynastids or Melolonthids.

To his own satisfaction, and to ours, he proved that the Mayagüez disease was not caused by white grubs, but that some people thought so indicates that these insects were present in the cane-field at that time and presumably caused some damage that might be confused with the disease proper. Yet they could not have been very abundant, for the extensive natural history collection of Dr. Stahl, containing several similar beetles from Cuba and Trinidad, had specimens of only one from Puerto Rico, which he had identified as *Ancylonycha crenaticollis* Blanchard, and one other of that genus without specific appellation. The list of Dr. Juan Gundlach, published in 1887–1894, covering his collections made previous to 1881, had no such name (pp. 621–623), or anything that might be thought to be the Puerto Rican May beetle, although in other respects it is much more complete than Dr. Stahl's list of his collections, published in 1882. Admittedly, Dr. Gundlach was not

interested in such small insects as leafhoppers or scale insects, but that he should have missed such large and conspicuous insects as May beetles seems incredible. It is possible that he did have specimens, but that, as these could not be specifically identified by his correspondents in Germany, they were not listed. Yet Dr. Gundlach was interested in the economic aspects of all insects, and rarely failed to note the damage they caused. If he did not include May beetles, one may presume that the economic aspect of their larval form was not noticeable at the time that he was here.

As one result of the devastation caused by the Mayagüez disease, Don Santiago McCormick went to Trinidad in 1879 to get new varieties of cane which would be resistant or immune to the disease. This was at a time when most of the British West Indies were bringing the mongoose, *Herpestes birmanicus*, from India in an attempt to control outbreaks of rats, and it is generally supposed that he brought back with him, in addition to the new cane varieties, several pairs of the predator. This was not the first introduction into Puerto Rico, however, for, according to Mr. Edmundo D. Colón (1930, p. 261), Don Guillermo Lamb brought some from Jamaica in 1877.

We have no exact information, then or at any later time, as to what the mongoose found to eat in Puerto Rico, but considering its present abundance, its impact on the fauna of the island at the time of its introduction must have been fundamental, and continues to be important. The mongoose is an omnivorous predator, and in those islands of the Lesser Antilles where the poisonous fer-de-lance, *Bothrops atrox*, was once exceedingly common, the beneficial effect of the mongoose in reducing its numbers almost to the vanishing point is undeniable. Elsewhere, any beneficial aspects of the introduction of the mongoose are much more than counterbalanced by those injurious to the interests of man. To some extent the mongoose may prey upon the rat, but since rats continue to exist in numbers but little diminished by its presence, its value in rat control is problematical. Its depredations on domestic poultry became at once appar-

ent, as well as less noticeable but more fundamentally injurious attacks on ground-nesting birds, most of which feed primarily on insects. Reputedly the mongoose may also eat large insects, but not in any large numbers when other more attractive food is available. Dr. J. G. Myers (1931) notes that not only snakes, but also toads and ground-lizards are killed. "Wherever the mongoose has become established, it tends to extirpate these lizards everywhere, save in the immediate vicinity of towns. This both Dr. Barbour (1930) and myself have observed in a number of the islands." Dr. Karl P. Schmidt (1928) found the ground-lizard "very abundant on Culebra, where the mongoose has not been introduced, while on Vieques the inhabitants informed me that the 'aldea' had exterminated the 'iguana' as well as the 'lucia' and the snakes."

The ground-lizard or "iguana" of Puerto Rico, *Ameiva exsul* Cope, spends only a comparatively short part of its time, around mid-day, above ground, being subterranean during most of its existence. It burrows readily through the soil, and has been found to eat both eggs and grubs of the May beetle (Wolcott, 1924). To what extent its food consisted of such items before the mongoose had so greatly reduced its numbers was not recorded at that time, and can not be determined now. It would be more difficult to believe that that importation of the mongoose so reduced the numbers of the ground-lizard as to permit an enormous increase in the numbers of white grubs if the obverse side of the picture were not a matter of fact and common observation: the practically perfect control of white grubs which eventually ensued when the giant Surinam toad became abundant in Puerto Rico. This required but ten or a dozen years, while thirty or forty years elapsed between the time of the introduction of the mongoose and maximum white grub injury. We may presume that at no time was the decrease in iguana population so pronounced as to be apparent, while the increase in white grub abundance was also so gradual that only newcomers to the island—cane men from Louisiana, Hawaii or Barbados—would consider

it so important that something must be done about it. Eventually, inspired by the example of the cane growers of Hawaii, in 1910 an experiment station was organized at Río Piedras, ostensibly to deal with all the problems affecting the production of sugar-cane, but primarily to cope with the white grub problem.

As a result of the investigations carried out at this station, it is possible to present a rather complete account of all the natural enemies of white grubs in Puerto Rico, including even the only observation on their being eaten by *Ameiva exsul*. In the more humid environment of the north coast, two Tachinid (Larvaevorid) fly parasites, *Cryptomeigenia aurifacies* Walton and *Eutrixoides jonesii* Walton, of which the females oviposit in the soft upper surface of the abdomen of the May beetle, exposed when the beetle is in flight, to some slight extent reduce the number of white grubs. Much more important is the larva of the luminous-eyed Elater or "cucubano," *Pyrophorus luminosus* Illiger, a predacious subterranean wireworm. To obtain nourishment for development to full size, the cucubano wireworm may suck the juice from five or six dozen white grubs, and pierce the skull of others merely for its apparent delight in the sport of killing (Wolcott, 1923). Several species of Scoliid wasps also attack the local white grubs (Box, 1925), but possibly because of the presence of hyperparasites such as Bombyliid flies, never become sufficiently abundant to make much impression on the white grub population. Dr. Alexander Wetmore (1916) found the local bare-legged owl or "mucaro," *Gymnasio nudipes*, to be the principal bird predator on May beetles, which, "by its nocturnal habit can successfully cope with the adults when they are flying," but he is forced to admit that it "was found most often in coffee plantations in the hills" and "on the south coast does not appear to be common." Of course he saw blackbirds picking up grubs in freshly plowed furrows, but this is only one time in the year when the birds have access to this form of subterranean food, and many grubs escape even when they follow the plow most

closely. Indeed, for practical purposes, one may say that white grubs had no natural enemies of importance on the south coast of Puerto Rico, and naturally one might expect that they would increase in numbers to the point where they would begin to exhaust the food available.

Extensive campaigns of hand-picking the grubs in fields being plowed, aided by pigs and blackbirds, and of hand-collecting of the May beetles at night from the leaves of sugar-cane and host trees were organized by all the Centráles, this being a stern necessity if the mills were to have any cane to grind. This was the reason why Guánica Centrále organized La Romana in the Dominican Republic, where white grubs were not a pest, and imported two or three boat-loads of cane a week during the grinding season. Ordinarily, sugar-cane can be ratooned many times before the stool is so weakened that replanting is necessary, but on the south coast of Puerto Rico the white grubs so completely destroyed the root system that replanting was essential for every crop. The account (Cotton, 1918) of the attempts at chemical control with what crude insecticides were available at that time is one of heart-breaking failure. No one could imagine the synthesis and commercial production of the heavily chlorinated organics, such as Aldrin and lindane, by means of which white grubs may be so effectively and inexpensively eliminated at the present time. The possibilities of biological control were apparently limited by the fact that these grubs were endemic species, of which Mr. E. G. Smyth (1917) characterized and named the largest species found in the eastern coastal region of Puerto Rico and on Vieques as *Phyllophaga portoricensis*, and its analogue in the western third of the island *Phyllophaga vandinei*. They were not foreign pests, of which control might be obtained by the importation of their natural enemies from their country of origin. Most of the parasites of white grubs are very specific in their host preferences; all those brought from abroad, either then or subsequently, failed of establishment (Wolcott, 1948). Apparently some predator less specific in its food requirements

was indicated, and Mr. Smyth seriously recommended the North American skunk!

> Large toads are found in most of the other West Indies and on the mainland, and keep the number of May beetles, and their larvae, the white grubs, so reduced that they are seldom pests to cultivated crops. Mr. D. W. May, of the Mayagüez Station, about four years ago obtained a dozen toads, *Bufo agua* Daudin, from Barbados, which were released here. They appear to be thriving and their descendants have been reported as far as four miles away from the point of release. Eventually, with an increase in their numbers, they will doubtless spread more widely over the Island, but it would be desirable to make other and large importations of this and other species from Barbados and elsewhere, and immediately begin to obtain the benefits in decreasing the numbers of white grubs which would ensue from their presence in the cane fields of Porto Rico (Wolcott, 1924).

This is the first published record of the introduction into Puerto Rico of the giant Surinam toad, *Bufo marinus* (Linnaeus), as the systematists subsequently decided this very definitely non-marine but exclusively fresh-water inhabiting and terrestrial species must be called.

Mr. May was singularly diffident about admitting his complicity in the introduction of "the toad, ugly and venomous," and rather doubtful that it "wears yet a precious jewel in his head"; although pragmatically translated into its vulgar applications to local conditions, this may be construed to mean that it has an almost insatiable appetite for the consumption of May beetles. It is the considered opinion of the writer that, as against all the carefully studied projects carried on at the Mayagüez Station during the many years that he was in charge, none was of greater benefit to the agriculture of Puerto Rico than was this: for such a long time unadmitted and unrecognized, and completed at so little expenditure of time, money and energy. Indeed, it was not until the value of the toad in the control of the changa and white grubs was generally apparent in the Mayagüez region that his official announcement (May, 1927) appeared.

In the meantime, quite independently and without knowledge of this first introduction, Mr. R. Menendez Ramos brought several pairs of the same species of toad from

Jamaica during the winter of 1922–23. It took all the time of one peon to collect food for these ravenous toads, and eventually they were released at Río Piedras. Presumably their descendants populated the eastern and northern coastal areas of the island as the progeny of those from Barbados occupied the western and southern sections, crossing and intermingling at many points.

The equable climate of coastal Puerto Rico is especially favorable for the development of *Bufo marinus,* being neither too hot in summer with a maximum of 97° F., nor too cold in winter with a minimum of 58° F. The central mountainous regions, occupied by tobacco and pineapple plantations, coffee groves and the remnants of virgin forest, are somewhat too cold at night, and even during the peak of its abundance, few toads were to be found at the higher elevations. The xerophytic south coast is in fact as desirable as the more humid north coast, for natural extensive shallow lagoons, as well as artificial reservoirs and drainage ditches, are available for the development of tadpoles. Exposed to tropical sunshine, the eggs of the toad hatch by the third day. The tadpoles feed on the slimy algal growth generally present on stones and vegetation in quiet water. As compared with the tadpoles of frogs, they lose their tails when still very small, and these " zapitos " begin terrestrial existence feeding on mites, springtails, just hatched caterpillars, nymphal leafhoppers and planthoppers and ants. Their capacity as well as their ability to eat more and more of larger and larger insects continues with their rapid increase in size, until eventually fully grown females are able to swallow adults of the sugar-cane rhinoceros beetle, *Strataegus barbigerus* Chapin (which Drs. Stahl and Gundlach referred to as *Strataegus titanus*), despite its comparatively enormous size, its horns and very spiny legs.

The considerably smaller May beetles are of a size to be eaten in quantity: they are easy to capture as they emerge from the soil at twilight and again towards daybreak as they again seek safety in the ground after having spent the night in feeding on the leaves of trees and in copulation.

On rainy nights, when the smaller black Scarabaeids of *Ligyrus, Dyscinetus* and *Parachalepus* may appear in large numbers, the great number of pellets of toad excrement to be found the following morning shows how extensive has been their consumption by toads (Wolcott, 1937). Millipedes of such common species as *Trigoniulus lumbricinus* (Gerstaecker) and *Orthomorpha coarctata* (Saussure) progress at a speed which makes their capture by the toad very simple, and they practically disappeared from the insular fauna when the toads were most abundant. Such luminous insects as fireflies and the "cucubano" could hardly escape destruction, so blatantly advertising their presence. The observations of Mrs. Raquel R. Dexter (1932) on the food habits of the toad proved how few beneficial insects were consumed, and started exportations that carried *Bufo marinus* first to Hawaii (Leonard, 1932), and subsequently around the world to many tropical islands and countries where it might be of value, as well as to other less favorable environments in which it could not survive.

The primary factor so greatly favoring its development in such enormous numbers in Puerto Rico was of course the apparently inexhaustible supply of food available. Despite the number of predacious insects and other animals feeding on tadpoles, and the enormous numbers of toads unavoidably slaughtered on rainy nights by passing automobile traffic, the toad could continue to develop in ever increasing numbers as long as food remained plentiful. But when the scarcity and eventually the entire absence of white grubs in cane fields being plowed all too plainly indicated that May beetles no longer existed in appreciable numbers to feed toads, all other sources of food had likewise disappeared. During three exceptionally dry years Cartagena and Guánica Lagoons completely dried up, and thus disappeared the most favorable environments for the development of tadpoles on the south coast. Rapidly the balance began to swing in the opposite direction. As the toads became scarce, again one might see an occasional "cucubano," an insect which for many years had completely dis-

appeared from the north coast and had survived only in the mountainous interior where the toads did not penetrate. Cane growers of a new generation, inexperienced in the plagues of white grubs that had infested the fields of their fathers, again began to complain about the abundance of white grubs. In 1948–49, the grubs of the "vaquita," *Diaprepes abbreviatus* Linnaeus, appeared in destructive abundance on the south coast, presumably indicating a greater consumption in fact of the adults by the toad than stomach and excrement pellet examination had shown. To those who can remember the enormous abundance of white grubs and "vaquita" grubs before *Bufo marinus* was brought to Puerto Rico, the present infestations seem quite minor. Indeed, the balance has already begun to swing in the other direction in some localities, and it may be presumed that with the lagoons of the south coast again full of water, and at least a fraction of the former abundance of May beetles present, the toad may again become reasonably numerous in another year or two.

The rather extensive use of soil insecticides very toxic to grubs, such as lindane and and octalene (now Aldrin), which were previously not available and are so new that the residual effects are as yet unknown, may alter the picture considerably. Were it not for this unpredictable factor, one might presume even shorter swings in the balance between toad versus white grub until a reasonably stable equilibrium is attained. The average level of abundance of white grubs will never be as low as before the introduction of the mongoose, and, conversely, it will never again be as high as before the introduction of the toad.

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THE DIFFERENTIAL RESPONSE OF MALE AND FEMALE GERM CELLS OF *SCIARA COPROPHILA* (DIPTERA) TO IRRADIATION

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INTRODUCTION

THAT the chromosomes of the sperm and oocyte of Sciara respond differently to X-rays was discovered by Metz and Boche (1939). These investigators found numerous rearrangements (salivary gland chromosomes) among the progeny of irradiated males, but none among the offspring of treated females.

Subsequent studies have shown that this differential response of the male and female germ cells is not a matter of sex, but one which depends on the condition of the chromosomes at the time of irradiation. Metz and Bozeman (1940), in their careful, painstaking work on the ovary of *S. ocellaris,* demonstrated that the oocyte chromosomes of this species are resistant to the rearrangement-inducing effects of irradiation from the beginning of oocyte growth in the early larva until ten hours after eclosion of the adult. During this entire period they found the chromosomes of the synchronously developing oocytes to be in a typical meiotic prophase, the paired homologues being long, slender threads fairly uniformly distributed throughout the nucleus (for photograph of this stage see Crouse, 1943, page 72, figures *n* and *o*). Reynolds (1941), working on the same species, showed that the ovarian egg becomes sensitive to X-rays the second day of adult life, and that the onset of sensitivity is correlated with the movement of the oocyte tetrads onto the first maturation spindle. As the first meiotic division progresses from metaphase to anaphase, the

oocyte chromosomes become increasingly sensitive, as determined by the percentage of rearrangements recovered and by egg hatchability (Reynolds, 1941; Metz and Bozeman, 1942).

Although the oocyte chromosomes become sensitive to the ionizing effects of irradiation during the first meiotic division, the kinds of rearrangements recovered in the F_1 are not the same as those recovered from irradiated sperm. In his study of X-rayed oocytes, Reynolds (1941) found inter-chromosomal exchanges to be very rare; among 16 rearrangements analyzed, there were 13 inversions, two deletions, and one translocation. This observation has been verified by the more extensive experiments of Metz and Bozeman (1942 and 1949). Irradiation of sperm yields quite a different result; of 28 F_1 aberrations studied by Metz and Boche (1939), 14 were inversions and 14 were reciprocal translocations.

The predominance of rearrangements of the intra-chromosomal type (inversions and deletions) in irradiated oocytes may be explained in one of two ways: either (1) broken non-homologous chromosomes in the oocyte nucleus fail to contact each other before restitution or intra-chromosomal rearrangement has occurred; or (2) non-homologous chromosomes in the oocyte nucleus exchange segments, but the translocated chromosomes are eliminated at meiosis (the first and second oocyte divisions in Sciara are completed after fertilization, which occurs when the egg is laid).

In order to determine which of the two explanations is correct, it is important to study the frequency with which reciprocal translocations are transmitted by females heterozygous for such translocations. A study of this sort has been made on *S. coprophila* (Crouse, 1943, and unpublished). The percentage of aneuploid eggs can be determined only very roughly on the basis of egg hatchability in Sciara. Adequate data are available for nine of the 19 translocations which have been studied in this species; these data place the frequency of aneuploidy at less than 50 per cent. Each of the 19 translocations studied was transmissible through the egg, and this in spite of the fact that three

chromosomes were reciprocally exchanged in two instances and all four chromosomes of the complement in another.

With the knowledge that reciprocally translocated chromosomes are readily transmitted through the egg of *S. coprophila,* the second theoretical explanation offered above can be eliminated as incorrect, provided, of course, that the oocyte of this species responds to irradiation in a manner similar to that of *S. ocellaris.*

The response of the oocyte of *S. coprophila* to X-rays was studied in the experiments described in this paper. Parallel studies performed simultaneously on irradiated sperm are also presented.

Materials and Methods

Two types of experiment were conducted. In both of them, adult females or adult males were X-rayed and mated to untreated individuals. Flies from the Wavy mutant stock [1] were used exclusively. The F_1 daughters derived from irradiated males or females were bred singly to untreated males, and the progeny from this cross (*i.e.*, the F_2 generation) was then examined by one of two methods.

In the first series of experiments, a cytological study was made on the salivary gland chromosomes of the F_2 larvae,[2] Gross rearrangements, including inversions and reciprocal translocations, were scored in this study; but minute alterations which involved only a few bands were omitted. No F_2 culture was considered "analyzed" until satisfactory preparations of eight larvae from the culture had been examined. It was necessary to examine as many as eight larvae, since only 50 per cent. of the zygotes in each F_2 culture possessed, in the case of any one of the four chromosome pairs, one homologue derived from the irradiated parent and one from the untreated male bred to the F_1 female.

[1] This stock was obtained from the Laboratory of Professor C. W. Metz, of the University of Pennsylvania.

[2] F_2 instead of F_1 larvae were analyzed in order that induced X-translocations could be maintained for subsequent study.

The second series of experiments was designed to detect only reciprocal translocations involving the sex chromosome. Previous studies (Crouse, 1943 and 1946) on translocations in this species had revealed a unique genetic effect (described below) produced by reciprocal exchanges of the X chromosome. Using this effect as a criterion, it was possible to examine, with considerable facility, large numbers of irradiated sperms and oocytes for induced reciprocal translocations involving the sex chromosome.

The genetic effect produced by X-translocations in *S. coprophila* which was referred to above, is an alteration in the sex ratio of the progeny of females heterozygous for such translocations. Ordinarily in this species, a female will produce either sons or daughters, but not both kinds of offspring. Whether she produces sons or daughters is determined by the genetic quality of her sex chromosomes. Females of XX constitution are male-producers; XX′ females are female-producers. The mutant gene Wavy is a dominant located on an X′ chromosome. In the Wavy stock, which was used in these experiments, there are two kinds of females, Wavy and wild-type; the former (XX′) produce daughters and the latter (XX) produce sons. If, however, a Wavy female is heterozygous for an X-translocation, she will produce sterile patroclinous sons in addition to the expected family of daughters; the percentage of patroclinous sons produced depends upon the particular X-translocation in question.

In the second series of experiments, therefore, the search for reciprocal translocations involving the sex chromosome was technically quite simple. Females of Wavy phenotype were used exclusively in the P_1 generation, and only the Wavy daughters (F_1) were bred in deriving the F_2. Upon emergence of the F_2 flies, each culture was examined for sterile exceptional males. The validity of this method of testing is confirmed by the fact that of the nine F_2 cultures which yielded such males (see Table 2), subsequent cytological study showed a reciprocal translocation involving the sex chromosome to be present in each case.

In the first series of experiments an attempt was made to determine whether the unlaid egg of *S. coprophila* is insensitive to the rearrangement-inducing effect of irradiation up to the second day of adult life, as in the case of *S. ocellaris* (see Introduction). Consequently, adult females of two different ages were irradiated. The females in one group (designated "young oocytes" in Table 1) were 43–45.5 hours old (*i.e.*, 43–45.5 hours after emergence at approximately 70° F.), and the females in the other group (designated "old oocytes" in Table 1) were 46–72 hours old at the time of treatment.

The dosage of X-rays applied to the adult males in both series of experiments was not the same as that applied to the adult females. Males irradiated at 4,000 r were found to yield approximately the same number of offspring as the "old" females irradiated at 2,000 r. Hence, dosages of 4,000 r and 2,000 r were used for the males and females respectively.

Results

The data collected in the two series of experiments are presented in Tables 1 and 2.

TABLE 1

Cytological Analysis of F_2 Larvae Derived from X-rayed Male and Female Germ Cells of *S. coprophila*

	No. Germ Cells Tested	No. Germ Cells Containing Rearrangements	No. Inversions	No. Translocations	No. Chr. Breaks
X-rayed (2,000 r) Young* Oocytes	15	0	0	0	0
X-rayed (2,000 r) Old* Oocytes	16	3	5	0	10
X-rayed (4,000 r) Sperm	16	4	2	2	8

*Two series of adult females were irradiated, one at 43-45.5 hours (young oocytes) after eclosion, the other at 46-72 hours (old oocytes).

TABLE 2

X-Translocations Induced in Male and Female Germ Cells of *S. coprophila*

	No. Germ Cells Tested	No. X-Translocations
X-rayed (2,000 r) Old Oocytes	42	0
X-rayed (4,000 r) Sperm	108	9

In the cytological study on F_2 larvae (Table 1) it was found:

(1) that the oocytes of *S. coprophila* between 43–45.5 hours of adult life yield no gross chromosomal rearrangements upon irradiation (2,000 r); whereas oocytes between 46–72 hours of adult life yield inversions when irradiated at the same dosage;

(2) that 2,000 r units applied to the "old" oocytes induce approximately the same number of breaks leading to gross rearrangements as 4,000 r applied to sperm (10 *versus* 8);

(3) that the breaks induced in "old" oocytes result only in intra-chromosomal rearrangement (inversions), whereas the breaks induced in sperm result in both inversions and reciprocal translocations. Of the five inversions induced in oocytes, one was in chromosome II, two in III and two in IV (for chromosome morphology of this species see Crouse, 1943); one of the inversions in IV was pericentric and it included practically the entire chromosome. Of the four rearrangements induced in sperm, the two inversions were located in chromosomes X and III respectively; and the two translocations involved II–III and X–IV;

(4) that the five inversions induced in oocytes were distributed among three of the sixteen oocytes tested. This fact is of considerable interest, for it means that although breaks were induced on non-homologous chromosomes in the same nucleus, the chromosome segments failed to undergo reciprocal exchange.

In the second series of experiments, where relatively large numbers of irradiated germ cells could be examined,

nine X-translocations were found among 108 sperm tested but none among the 42 oocytes examined (see Table 2). The exact P value of this difference, as measured by chi-square, is 0.094.

Discussion

It was stated above (Introduction, page 195) that the predominance of rearrangements of the intra-chromosomal type in irradiated oocytes of *S. ocellaris* may be explained in one of two ways; but that in the absence of cytogenetic studies on reciprocal translocations in this species, it is not possible to choose between the two alternatives. In *S. coprophila,* reciprocal translocations are known to be readily transmitted through the oocytes of females heterozygous for such translocations. The experiments presented in this paper show that the oocyte of *S. coprophila* responds to X-rays in a manner similar to the oocyte of *S. ocellaris;* the irradiated oocytes yielded inversions but no translocations. In view of these experiments, therefore, it would appear that the failure to recover translocations in irradiated oocytes in this genus results not from the loss of such rearranged chromosomes at meiosis but rather from the failure of non-homologous chromosomes to contact each other before restitution or intra-chromosomal rearrangement has occurred.

Summary

Comparative studies have been made on the response of male and female germ cells of *S. coprophila* to irradiation.

(1) When adult females are exposed to X-rays 43 to 45.5 hours after eclosion, no gross rearrangements of any type are recovered; but oocytes irradiated between 46 and 72 hours of adult life yield inversions.

(2) Approximately the same number of breaks leading to gross rearrangements are induced by 2,000 r in oocytes and 4,000 r in sperm.

(3) Irradiation of sperm results in both reciprocal translocations and inversions.

(4) Tests for reciprocal translocations involving the X chromosome yielded nine such translocations among 108 sperm tested but none among the 42 oocytes examined.

(5) The failure to recover inter-chromosomal exchanges following irradiation of oocytes is discussed.

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AN ANALYSIS OF CERTAIN DIMENSIONAL RELATIONSHIPS OF THE VIRGINIA OYSTER, *CRASSOSTREA VIRGINICA* (GMELIN)[1]

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Studies of dimensional variation in individuals of a species existing under similar and dissimilar environmental conditions possess taxonomic and ecologic interest. Special interest centers in the edible oyster of the Atlantic Coast because of the great variation within the species and the divergent views as to its generic status. Most oyster biologists have referred to the Virginia oyster or the American oyster as *Ostrea virginica* Gmelin.

Nelson (1938) in his classical study of the development of the promyal chamber in the spat of *O. virginica* proposes to place "all flat hermaphroditic larviparous oysters without a promyal chamber in the genus *Ostrea* and to refer to the genus *Gryphaea* all the deep-cupped oviparous oysters with the promyal chamber." In this proposal he supports the view of Orton (1928) who pointed out the existence of two distinct types worthy in his opinion of generic or subgeneric rank. Nelson (*loc. cit.*) stresses the importance of the promyal chamber and of the marked morphological differences between the two types and advocates full generic rank for the two types. Under this plan the common American oyster becomes *Gryphaea virginica* or, according to Gunter (1948) more properly *Crassostrea virginica* (Gmelin), that is used here.

The extent of modifications of the shell by environmental

[1] This study was conducted at the Virginia Fisheries Laboratory and the College of William and Mary during the period 1945–46. The data have been analyzed and prepared for publication at and with the aid of the Cranbrook Institute of Science, Bloomfield Hills, Michigan.

influences led Nelson to suggest that the anatomy of the soft parts also be considered in the taxonomy of the oyster. We have felt that, in addition to the above, attention should be given to the relations between linear, weight and volume measurements of populations of the same species living in different habitats. In this connection Gunter (1938) has evaluated the length–width ratios of different sizes and from different environments. His findings are of particular interest in relation to our growth dimensional data on the Chesapeake oysters.

The measurements upon which this paper is based were made by Miss Elizabeth Overcash working at the Virginia Fisheries Laboratory and the College of William and Mary under the direction of the writer. Acknowledgment is also made to Professor Paul S. Dwyer, of the University of Michigan, who provided most valuable assistance in the presentation of the data.

Methods

Oysters for comparative purposes were collected in the main from uncultivated grounds (public "rocks") in the York and Rappahannock Rivers, tributaries of Chesapeake Bay. The samples were taken with a dredge. Following the collection of each sample, some selection was necessary in order to have specimens for dimensional measurements that could be opened without significant breakage of the shells. However, relatively few oysters were rejected.

The following measurements were made: length, width, total weight, total volume, shell weight, shell volume, wet weight and dry weight of body tissue. The volume of the cavity of the oyster, termed inner volume, was obtained by subtracting shell volume from total volume. Volume was determined by the overflow displacement method described by Overcash (1946) who made all the measurements upon which this discussion is based. The thickness of the shell was not measured; hence only length and width were used

in those formulas in which volume was estimated from linear measurements. Numerically small samples were collected from eight different oyster grounds. Two of these samples were from Towle's Point (salinity 10–13 °/₀₀) in the Rappahannock River off the mouth of the Corrotoman River tributary and Mobjack Bay, a tributary of Chesapeake Bay immediately north of the mouth of the York River. These collections were small for most purposes, the value of n in each case being 7 (Tables I and II). In addition to the afore-mentioned eight samples, three relatively large collections were taken. One of these was taken on April 19 (salinity 16.8 °/₀₀) from Parrott's Rock ($n = 39$) in the Rappahannock River. The range in length was 52 to 94 mm. and in total weight, 20–99 gm. The remaining two samples came from a large York River oyster "rock" situated between King and Indian Field Creeks. The dates when these samples were taken are November 25, 1945, and February 22, 1946, the corresponding salinities being 18.5 and 12.8 °/₀₀. For purposes of analysis these two sets of data have been thrown together and treated as one group ($n = 146$). The length range of this group was 71–138 mm. and the range of total weight was 60 to 260 gm. The entire ten groups are listed in Table II, and the principal statistical procedures employed in this paper are given in Snedecor (1946, pp. 215–252) and Thurstone (1947, pp. 259–281).

Results

A comparison of the values of the constants a and b in the prediction equation $Y = a + bX$ is given in Table I. Reference to Fisher (1928, p. 176) indicates that in Table I groups 2, 3 and 8 have values of r that are significantly different from zero within the 1 and 5 per cent. levels. In general, the degree of variation is of such magnitude that more measurements are needed to get more stable measures of r. Group 6 was collected in an entirely different environment from the remaining groups and gives evidence of a relatively high degree of variation. The extremely low

TABLE I

Constants a and b in Equations of Type $Y = a + bX$ Expressing Size Relationships in *Crassostrea Virginica* (Gmelin), Collected from Different Oyster Ground in the Chesapeake Bay Area. Y = Inner Volume; X = Dry Weight.

Group No.	Name of oyster ground	Location	Date of collection 1945	Inner vol. range in mls	Extent of range in mls	Approxim. salinity in ‰	Depth in feet	n	a	b	r	σ_E
1	Aberdeen Rock	15 miles above mouth of York River	March 20	18.5-38.5	20.0	15-17	5-8	10	21.224	3.198	0.306	5.21
2	Page's Rock	2 miles below Aberdeen Rock	March 5	14.5-26.5	12.0	16-18	3-5	17	10.130	5.963	0.667	2.54
3	Intertidal area	Back Creek near mouth of York River	April 9	9.7-32.3	22.6	18-20	Intertidal	11	6.098	8.446	0.614	5.16
4	Parrott's Rock	15 miles above the mouth of the Rappahannock River	March 29	9.7-29.7	20.0	14-17	12-18	16	11.674	4.861	0.439	5.28
6	Burton's Bay	Off Wachapeague on the Seaside of Virginia	March 17	29.0-56.0	27.0	25-30	Intertidal	13	44.934	-0.860	-0.067	8.54
8	Middle Ground	Mouth of Wicomico River	March 19	12.0-30.5	18.5	12-15	2-6	14	6.096	8.710	0.781	3.48

TABLE II

Summary of Various Oyster Distributions in Respect to Dry Weight–Inner Volume Ratios. X= Individual Ratios

Group No.	Oyster Ground	Value of n	ΣX	ΣX^2	$\bar{X}$
1	Aberdeen Rock, York River	10	0.6224	0.0425	0.0622
2	Page's Rock, York River	17	1.4117	0.1210	0.0830
3	Intertidal area, York River	11	0.9173	0.0840	0.0834
4	Parrott's Rock, Rappahannock	16	1.4996	0.1552	0.0937
5	Towle's Pt., Rappahannock River	7	0.6328	0.0616	0.0904
6	Burton's Bay, Seaside	13	0.8981	0.0674	0.0691
7	Mobjack Bay	7	0.5182	0.0405	0.0740
8	Wicomico River	14	1.1159	0.0934	0.0797
9	Rappahannock River (large group)	39	3.5480	0.3506	0.0910
10	York River (large group)	146	12.7159	1.2448	0.0871
Σ	All grounds	280	23.8799	2.2611	0.0853
Σ	4 York River groups	184	15.6673	1.4923	0.0851
Σ	3 Rappahannock River groups	62	5.6804	0.5674	0.0916

Analysis of Variance

Source of Variation	Degrees of Freedom	Sum of Squares	Mean Square	F	P
		All groups (1-10)			
Total	279	0.22435			
Between means of groups	9	0.01316	0.00146	1.87	>.05
Within groups	270	0.21119	0.00078		
		York River groups (1, 2, 3, 10)			
Total	183	0.15824			
Between means of groups	3	0.00594	0.00198	2.34	>.05
Within groups	180	0.15230	0.00085		
		Rappahannock River groups (4, 5, 9)			
Total	61	0.04696			
Between means of groups	2	0.00007	0.000035	<1	>.05
Within groups	59	0.04689	0.000795		

value of r for this group, namely -0.067, is attributed mainly to three measurements in which the dry weight was exceedingly low.[2]

Analysis of variance has been employed to estimate whether or not the different samples may be regarded as coming from a homogeneous population on a basis of the dry weight–inner volume ratios. It would be of interest to know if the variation "between" sample ratio means is significantly greater than the variation within the samples. To throw light on this point we have calculated the ratio of the "between" variance to the "within" variance and designated this ratio F. Thus, for the ten samples ($n = 280$) $F = 1.87$ and $P > .05$ (Table II). The evidence does not prove conclusively that the sample ratio means vary more than would ordinarily be expected if they were taken at random from a homogeneous oyster population. Analysis for variance in the four York River groups ($n = 183$) and in the three Rappahannock River groups ($n = 61$) was also made. In each case the probability as denoted by P was found to be greater than .05, indicating that there was no difference in the ratios that could not be explained on a basis of random sampling.

In addition to the test on means, a study of the homogeneity of the variance of the ratios was made using Bartlett's test (Snedecor, 1946, p. 250). This test of homogeneity applied to all ten groups taken together resulted in a chi-square with $.01 < P < .05$. The four York River groups gave a P value less than .01 indicating heterogeneity. However, the three Rappahannock River groups yielded a value for P greater than .05; hence there is no proved heterogeneity of variance here (Table III).

Attention may now be turned to the variances in the two individual dimensions, namely, inner volume and dry weight. It is shown in Table IV that on a basis of the data

[2] This condition may represent a normal relation or one brought about by the presence of an oyster crab feeding on the meats within the cavity of the oyster. But, of course, such a possibility is not confined to the seaside oysters.

TABLE III

Computation of Bartlett's Test of Homogeneity of Variance in Respect to Dry Weight—Inner Volume Ratios of *Crassostrea virginica* (Gmelin).

Number of groups	Degrees of Freedom $K-1$	χ^2	P
	All Groups (1–10)		
10	270	19.027	.01<p<.05
	York River Groups (1, 2, 3, 10)		
4	180	11.58	<.01
	Rappahannock River Groups (4, 5, 9)		
3	59	0.485	>.05

the group means do vary more than would ordinarily be expected if they were drawn at random from a homogeneous population. It was also found that the four York River groups and the Rappahannock River groups likewise differ

TABLE IV

Analysis of Variance in Oyster Distributions with Respect to Dry Weight (X) and Inner Volume (X_1) Dimensions

Source of variation	Degrees of freedom	Sum of squares		Mean square		F		P	
		X	X_1	X	X_1	X	X_1	X	X_1
		All Groups (1-10)							
Total	279	48643.0	381.26						
Between means of groups	9	19488.0	123.21	2165	13.690	20.05	14.32	<.01	<.01
Within groups	270	29155.0	258.05	108	0.956				
		York River Groups (1, 2, 3, 10)							
Total	183	31045.0	271.364						
Between means of groups	3	5143.0	47.870	1714.3	15.957	11.91	12.85	<.01	<.01
Within groups	180	25902.0	223.494	143.9	1.242				
		Rappahannock River Groups (4, 5, 9)							
Total	61	3372.4	37.027						
Between means of groups	2	1582.4	12.506	791.2	6.253	26.08	15.05	<.01	<.01
Within groups	59	1790.0	24.521	30.34	0.416				

TABLE V

Computation of Bartlett's Test of Homogeneity of Variance in Respect to the Dry Weight (X) and Inner Volume (X_1) Dimensions of *Crassostrea virginica* (Gmelin)

Number of groups	Degrees of freedom	χ^2		P	
		X	X_1	X	X_1
	All Groups (1-10)				
10	270	94.0	77.0	<.01	<.01
	All Except Large York River Group (Groups 1-8)				
9	125	16.0	12.0	approx. .05	>.10

significantly among themselves in so far as these two dimensions are concerned.

Bartlett's test for homogeneity of variance in respect to the dry weight and inner volume dimensions indicates that, on a basis of data obtained during this study, there is not a significant difference in variation for the nine groups, excluding the large York River group, but there is a significant difference when all are considered (Table V).

The largest collections were from Parrott's Rock ($n = 39$) on the Rappahannock River and near Indian Creek ($n = 146$) in the York River. Since $t < 1$, it appears that the inner volume relative to dry weight of meat is not significantly different in these groups of oysters. The values of the correlation coefficient are large enough to suggest an

TABLE VI

Constants a and b in Equations of Type $Y = a + bX$ Expressing Size Relationships in *Crassostrea virginica* (Gmelin). L W = Length Times Width; I V = Inner Volume; S V = Shell Volume; S W = Shell Weight; D W = Dry Weight.

Y	X	York River n =132				Rappahannock River n = 39			
		a	b	r	σ_E	a	b	r	σ_E
I V	D W	12.880	7.354	.684	3.36	6.180	6.249	.746	9.53
S W	L W	-15.5409	0.02117	.832	25.81	-23.651	0.01812	.861	9.466
S V	L W	-10.0354	0.009818	.857	10.78	-10.203	0.008073	.854	4.359
I V	L W	- 3.8838	0.005288	.774	7.90	- 3.848	0.004619	.810	2.957
D W	L W	- 0.2665	0.0004422	.655	0.933	- 0.716	0.0005132	.753	0.395

approximation to a straight line relationship. With the exception of the length/width–dry weight relation for the York River oysters, there are higher correlations between length/width and the remaining four measurements of size, the range of r being from 0.753 to 0.861 (Table VI).

An analysis of the relations between the several dimen-

TABLE VII

Factor Analysis of Intercorrelations of Linear Weight and Volumetric Data Based on the Measurements of 132 Oysters Ranging in Length from 71 to 138 mm. a_1 = Common Factor Variance. York River Oysters Collected Near Indian Creek.

Intercorrelations

A

	Total Weight	Total Volume	Length-Width	Shell Weight	Shell Volume	Inner Volume	Dry Weight
	–	.911	.840	.982	.957	.791	.734
	.911	–	.886	.950	.957	.878	.758
	.840	.886	–	.832	.857	.774	.655
	.982	.950	.832	–	.961	.749	.706
	.957	.957	.857	.961	–	.704	.705
	.791	.878	.774	.749	.704	–	.684
	.734	.758	.655	.706	.705	.684	–
				B			
a_1	.969	.997	.886	.960	.951	.829	.758
				C			
	–	-.055	-.019	.052	.035	-.012	-.001
	-.055	–	.003	-.007	.009	.051	.002
	-.019	.003	–	-.019	.014	.040	-.017
	.052	-.007	-.019	–	.048	-.047	-.022
	.035	.009	.014	.048	–	-.084	-.016
	-.012	.051	.040	-.047	-.084	–	.056
	-.001	.002	-.017	-.022	-.016	.056	–

sions by means of a partial correlation treatment failed to yield anything of interest. However, it was found that Spearman's theory of a single common factor fits reasonably well to this problem (Thurstone, 1947, pp. 259–281). The correlations given in Table VII A are determined by the single factor loading a_1 in B with errors of the order shown in C. It appears from this that a general factor, which we

might call size, is the dominant factor common to these variables.

Discussion and Summary

Oyster studies by numerous investigators have shown directly or indirectly that variation is a relatively dominant characteristic of this bivalve in comparison with marine or fresh-water clams. The need for information on such variation is generally recognized. Physiological experiments aiming to demonstrate the feeding behavior or the nutrient content of oysters growing under different environmental conditions are dependent on an understanding of the little understood factor, variation. This paper considers possible variation in widely separated environments. But, it now seems clear that the oyster is highly responsive to the immediate environment and one encounters variation in form and growth on a single oyster ground that may exceed that produced by the differences characterizing an entire river system. Improvements in oyster culture may depend to no small extent on an ecological study of the response of the oyster to slight differences in the immediate environment.

Table I suggests that oysters from a particular ground possess meat weights that are correlated with the volume of the cavities containing the meat. For a definite conclusion, larger numbers of measurements are required. All samples were collected during the colder seasons when the oyster is relatively inactive. Greater variation would be expected during the summer period (Galtsoff, Chipman, Engle, and Calderwood, 1947).

The dimensions of inner volume and dry weight are regarded to be reliable indices of size, hence they may be used for analyzing different populations in which these variables are correlated. Hopkins (1937) used a formula based on the inner volume–dry weight ratio for expressing the condition of oysters and a slightly modified formula was also employed by Medcof and Needler (1941). Recently, Ingle (1949) has presented valuable data suggesting the possibility of a significant correlation between the dry weight–

inner volume ratio and the glycogen content of the oyster. Analysis for variance in respect to the dry weight–inner volume ratios failed to reveal any ratio differences that could not be explained on a basis of random sampling. It is possible, however, that a larger number of records for each area might reveal significant differences in the ratios (compare Gunter, 1938).

In so far as the individual dimensions of dry weight and inner volume are concerned, the data indicate significant differences in variance between the several groups from the same river.

On a basis of the two large groups from the York and Rappahannock Rivers, it has been demonstrated that the difference in the dry meat weights per unit of volume of the inner cavity is not statistically significant (Table VI). Reasonably high correlations were obtained between the product of length times width and the four remaining indices of size, values of r for the Rappahannock group being somewhat higher than those for the York River oysters.

The application of Spearman's theory of a single common factor to the linear, weight and volumetric data is clearly demonstrated by the inter-correlations for the York River data given in Table VII.

The linear ratios of length to width for the two large groups (numbers 9 and 10, Table II) from the Rappahannock and York Rivers were found to be 1.426 and 1.512, respectively. On a basis of the value of t there is a significant difference at the 1 per cent. level. Gunter (1938) presents interesting data relating this ratio to environmental conditions, size and certain body characteristics. In the case of oysters from Matagorda Bay, Texas, he found that "small round" and "market size round" oysters had length–width ratios of only 1.16 and 1.25, respectively.

One of the most extensive sets of data dealing with size characteristics of oysters at different ages is that provided by Loosanoff (1947, p. 223) who studied the oysters of Long Island Sound, New York. He has shown that during the

first growing period oysters increase in length and width more rapidly than in depth. However, during the following year this relation was reversed. Loosanoff was able to demonstrate that in oysters which had completed their third growing season the meats constituted 13.7 per cent. and the shells 67.6 per cent. of the total weight. The corresponding percentages for oysters in the oldest group (8 to 13 years old) were 10.1 and 80.3 per cent. The York River data have shown a similar trend toward a decrease in the percentage weight of meats and an increase in the percentage weight of shells with increase in age.

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HAEMODYNAMIC FACTORS IN THE EVOLUTION OF THE DOUBLE CIRCULATION IN THE VERTEBRATES

DR. R. F. EWER

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In most text-books the evolution of the double circulation, with its complete separation of pulmonary and systemic circuits, is treated purely from the point of view of efficiency of oxygen transport. In mammals and birds the complete separation of right and left sides of the heart gives an equally complete separation of oxygenated and deoxygenated blood. In the amphibian and reptilian circulations the separation is only partial, and is usually presented as being "inefficient," without further discussion: for instance, Hyman (1942), referring to the circulatory system of reptiles, states that "this arrangement is impractical, since it allows mixing of venous and arterial blood."

This inefficiency in oxygen transport is, however, a necessary stage in the evolution of pulmonary respiration. The crocodile presents one of the most striking examples of such inefficiency, and may conveniently be considered first. Here (Fig. 1a) there is a complete separation of the two ventricles; the right systemic trunk arises from the left, and the pulmonary artery from the right ventricle. This arrangement offers the possibility of a complete separation of oxygenated and deoxygenated blood, but the possibility is not realized. The right systemic carries only oxygenated blood, but the left systemic arises together with the pulmonary artery from the left ventricle, and so delivers deoxygenated blood into the systemic circulation. In other reptiles the

first growing period oysters increase in length and width more rapidly than in depth. However, during the following year this relation was reversed. Loosanoff was able to demonstrate that in oysters which had completed their third growing season the meats constituted 13.7 per cent. and the shells 67.6 per cent. of the total weight. The corresponding percentages for oysters in the oldest group (8 to 13 years old) were 10.1 and 80.3 per cent. The York River data have shown a similar trend toward a decrease in the percentage weight of meats and an increase in the percentage weight of shells with increase in age.

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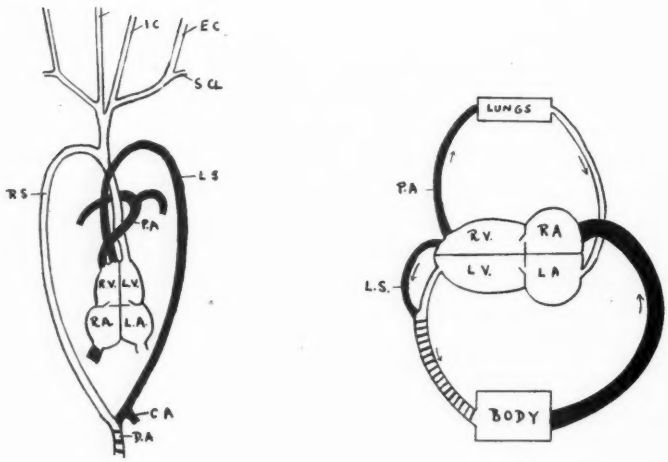


(a) (b)

FIG. 1. (a) The heart and arterial arches of a crocodile. (b) The crocodile circulation represented diagrammatically. Oxygenated blood, white; deoxygenated, black; mixed, striped.

C.A.	coeliac artery	L.V.	left ventricle
D.A.	dorsal aorta	P.A.	pulmonary artery
E.C.	external carotid artery	R.A.	right auricle
I.C.	internal carotid artery	R.S.	right systemic
L.A.	left auricle	R.V.	right ventricle
L.S.	left systemic	S.CL.	subclavian artery

condition is similar except that the ventricular septum is incomplete. Considered only in the light of oxygen transport the left systemic arch appears to be not merely useless, but positively deleterious.

Barcroft (1938) has pointed out that in biological inquiries it is rarely desirable to assume that a phenomenon is without significance. It is more profitable to bear in mind that in the hard school of natural selection the useless or harmful modification is unlikely to be preserved. More stands to be discovered if an organ or process, whose function is not immediately obvious, is submitted to very careful scrutiny and experiment before a verdict of "useless" is pronounced. The fact that sometimes erroneous func-

tional explanations are advanced does not invalidate Barcroft's attitude. Further investigations, and above all experimental testing of hypotheses, will dispose of those that are erroneous: but uncritical acceptance of "uselessness" will lead nowhere.

In the present case considerations of oxygen transport throw no light on the function of the reptilian left systemic; clearly then we must seek for an explanation on other terms; and as soon as we do so the answer becomes obvious. The double circulation can only work provided the lungs are capable of dealing with the same volume of blood per unit time as is the whole systemic circulation. Lungs of such dimensions certainly were not evolved suddenly in one step. It therefore follows that as long as the lung capacity is insufficient to deal with the total blood volume some mixing of oxygenated and deoxygenated blood must take place if the system is to work at all. The function of the reptilian left systemic now becomes apparent. The right side of the heart receives the whole venous return from the body: the left systemic acts as a shunt, and transfers back to the systemic circuit the excess with which the lung can not cope. These relations are shown diagrammatically in Fig. 1b. In addition the foramen Panizzae linking right and left systemics presumably allows equalization of blood pressures between the two arches. From Fig. 1a it can be seen that the head, and therefore the brain, receives only oxygenated blood from the right systemic, while the left systemic delivers its deoxygenated blood partly direct to the gut via the coeliac artery and partly into the dorsal aorta running posteriorly to the trunk. Far from being inefficient, this is the most adequate arrangement possible as long as the lungs remain insufficiently capacious to deal with the same minute-volume of blood as the systemic circulation carries.

The circulatory system of the birds can easily be derived without functional discontinuity from the reptilian condition. As the lungs become larger and capable of dealing with a greater and greater volume of blood so the left

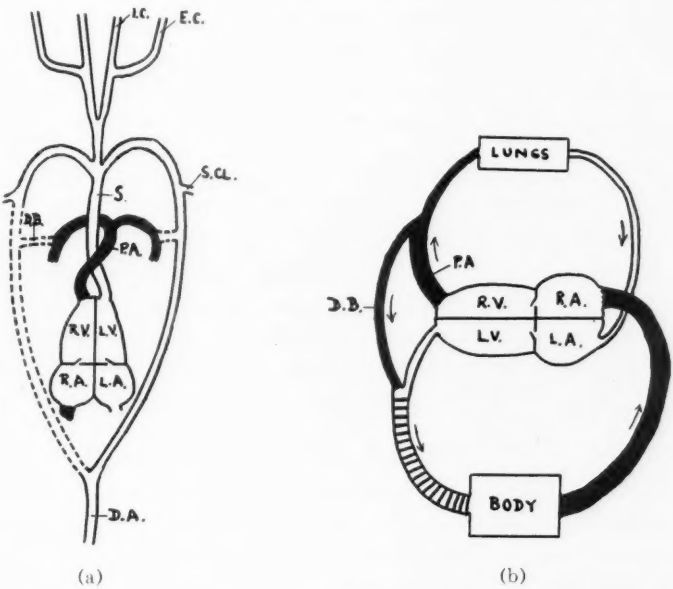
systemic is gradually reduced, carries less and less blood, and is finally lost altogether.

The condition in mammals is entirely different, and can not be derived from the arrangement found in the living reptiles. The single systemic trunk in the mammalian line never became divided into separate left and right roots. In development the single systemic trunk branches symmetrically to left and to right as it does in the Amphibia and later the right branch is reduced and finally obliterated (see Fig. 2a). The single systemic trunk arising from the left ventricle carries only oxygenated blood, and there is thus a complete double circulation. Looking at the adult mammalian circuit from the haemodynamic aspect we must ask how it worked before the lung had become large enough to deal with the whole volume of circulating blood. If no separate left systemic existed to act as a shunt where did the excess blood from the venous return to the right side of the heart go? This question can not be definitively answered, since it involves deciding what was the condition of the arterial arches in the extinct ancestors of the mammals, but a very plausible suggestion can be made. The ductus arteriosus (= ductus Botalli), linking the pulmonary artery with the aorta is present in the embryo of mammals, and is only closed off at birth. It seems entirely reasonable to suppose that this connection existed in the adults too of the ancestors of the mammals, and through it the excess blood passed from the pulmonary circuit to the aorta (Fig. 2a and b).[1] From this arrangement the mammalian condition can be derived by gradual increase in

[1] The embryonic pulmonary and systemic circuits are, of course, not only connected by the *ductus arteriosus;* they also communicate with each other via the *foramen ovale.* This latter connection, however, is regarded as an embryonic adaptation of secondary origin. To postulate its existence in the adult ancestral mammals rather than the persistence of the phylogenetically older *ductus arteriosus* seems unjustifiable on general grounds. In addition a shunt via the *foramen ovale* would result in a general mixing of oxygenated and deoxygenated blood, while the shunt via the *ductus arteriosus* excludes the deoxygenated blood from the supply to the brain, and is therefore the more physiologically efficient arrangement.

lung capacity accompanied by decrease in size and finally closure of the ductus arteriosus.

Thus by two somewhat different routes complete double circulations have been evolved in birds and in mammals. As far as oxygen transport is concerned these double circuits are just as effective as, but in no way superior to, the single



(a) (b)

FIG. 2. (a) The suggested condition of the heart and arterial arches in the ancestors of the mammals. The vessels shown in dotted lines are present in the embryos, but disappear in the adults of living mammals. (b) The circulation of the same represented diagrammatically. Oxygenated blood, white; deoxygenated, black; mixed, striped. D.B.—ductus arteriosus or ductus Botalli; S.—undivided systemic trunk; other letters as in Fig. 1.

circulation of the fishes. Haemodynamically, however, the double circuit is much more effective. The fall in pressure which occurs in the respiratory capillaries is made good by the second transit through the heart, and thus the oxygenated blood is distributed to the tissues at a higher pressure than is possible in the fish's single circuit. This is probably

a necessary prerequisite for the evolution of efficient terrestrial tetrapoda. With a single circuit the blood on its way to the limbs would traverse the respiratory capillaries, with a consequent fall in pressure. It seems unlikely that in these circumstances an adequate venous return could have been maintained from the long limbs of a cursorial mammal, and so terrestrial tetrapoda might have been compelled to remain crawlers rather than runners, and our own mode of locomotion out of the question.

In the case of the reptilian left systemic an exclusive preoccupation with considerations of oxygen transport has resulted merely in a failure to appreciate a functional role which should otherwise have been very obvious. There is, however, another case in which this one-sided approach has led into positive error; namely, the classical text-book account of the action of the spiral valve in the truncus arteriosus of the frog. It is generally stated that in the frog's ventricle there is only slight mixing of oxygenated and deoxygenated blood, and that the spiral valve acts as a sorting mechanism, distributing deoxygenated blood to the pulmonary circulation and oxygenated to the general body circulation. Recent experimental investigations by Foxon (1947) and Foxon and Walls (1947) have shown that this is incorrect, and that there is in fact no selective distribution of oxygenated and deoxygenated blood. No alternative function has as yet been proposed for the spiral valve, but considerations in terms of blood pressure adjustments might prove fruitful.

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A VACATION PORTRAIT OF THE AMERICAN NATURALIST W. H. DALL

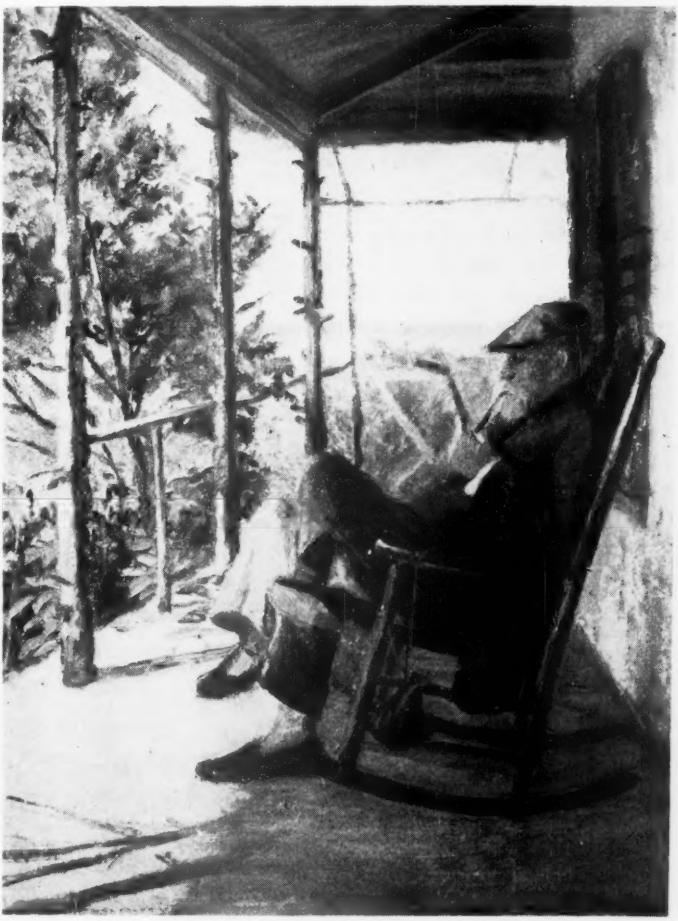
GEORGE HOWARD PARKER

William Healey Dall was born in Boston, Massachusetts, August 21, 1845, and died in Washington, District of Columbia, March 27, 1927. As a boy he attended the Boston Latin School, and his formal education did not progress much beyond this point. We are told that he early possessed a copy of Gould's "Invertebrata of Massachusetts" which did much to confirm his interest in local shells, an interest that is said to have brought him into personal relations with Dr. Gould and Professor Louis Agassiz. About the time of the Civil War he moved from Boston to Chicago where he formed an intimate acquaintanceship with William Stimpson and Robert Kennicott, two well-known local naturalists. When the Atlantic submarine telegraphic cable was threatened with failure, Dall was sent to Alaska to lay out a telegraph line, chiefly over land, from America across Asia to Europe. In 1868 on the success of the Atlantic cable he returned from the North and in 1870 published "Alaska and Its Resources." Thus was founded his life interest in this northern territory, an interest which centered especially in the remarkable molluskan fauna that occurs in that region.

During the latter part of Dall's life he was accustomed to spend a part of each summer at the Half-Way House on the southwest ridge of Mount Monadnock in Jaffrey, New Hampshire. In fine weather he and his wife were commonly to be found sitting on the southern porch of this

well-known inn reading the daily papers or other matters brought to them by the single mail delivery that reached the house each day. While Dr. Dall was at this inn a young woman of considerable artistic ability came there and among the sketches that she made was one in oil of Dr. Dall in his usual position on the porch reading the daily news. When she left the inn she gave this picture to the Finnish proprietress of the house, Mrs. Exel, who hung it on the wall of the living room on the ground floor of the inn. Here it became a familiar object of interest and was known to almost everyone who stopped for any length of time at the house as a portrait of Dr. Dall. When the house changed hands this portrait and many other small objects, mostly the property of Mrs. Exel, drifted into the attic. From time to time these things, with the consent of their owner, were sold off and it was from this omnium gatherum that I purchased from Mrs. Exel the picture of Dr. Dall used as the illustration in this article. As I had known Dr. Dall intimately during his life I valued the portrait as a personal remembrance of him. In the lower right-hand corner of it can be seen the name of the artist, E. Purdie, easily visible even in the reproduction in this paper. Moreover any one who knew Dr. Dall in his later days will be struck by the agreement between his features and those in this picture. Thus was Dr. Dall's portrait recovered from the attic of the Half-Way House and brought into the light again.

When this picture is looked at in detail the vacation composure of it is unquestionable. Dr. Dall's cap and pipe are indicative of an off-season leisure and the tobacco pouch hanging from the arm of his easy chair suggests repose. The whole equanimity of the scene indicates summer vacation and invades the picture in many other ways. In the sketch Mrs. Dall is almost hidden from view by her husband and in the original picture the bit of western sky carries in its tint an afternoon glow. All in all the scene seems to be the quiet close of a late summer day and is not suggestive of the hurry and bustle that is the ordinary part of the activity of a summer resort in full season. Thus rest



Photographic copy of an oil sketch of Dr. William Healey Dall, seated on the south porch of the Half-Way House on Mount Monadnock, Jaffrey, New Hampshire. The sketch was made by E. Purdie and is now in the possession of George Howard Parker.

and quiet are parts of the picture, features very characteristic of Dr. Dall's maturity and known to everyone as a most valued element in the atmosphere of Monadnock's Half-Way House. This might be regarded as an excellent advertisement of this house to those who seek such a feature in a mountain resort. Not so simple, however, is the fate of Dr. Dall's oil portrait! Even so quiet a sketch as this of an American natural historian deserves a place in a collection of portraits of such men and it is the hope of the present owner that the original painting will find itself eventually in some collection of portraits of American naturalists.

CAMAROSAURUS ANNAE—A NEW AMERICAN SAUROPOD DINOSAUR

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EXAMINING a group of Dinosaur bones from the collections of the Carnegie Museum of Pittsburgh, a graduate assistant, Mr. L. L. White, called attention to a dorsal vertebra (C.M. 8942) that seemed strikingly different from other Dinosaur dorsals. Describing it below as belonging to a new Sauropod species, the diagnostic characters are the absence of pleurocoels on the vertebral centrum combined with the presence of a low bifid neural spine with widely diverging branches.

The only known Dinosaurs possessing dorsal vertebrae with bifid spines and centra without pleurocoels are the two species of the genus *Dicraesaurus, D. hansemanni* and *D. sattleri,* described by Janensch from Tendaguru, East Africa. However, the acoelous centra and the long, erect and almost parallel spine branches of the dorsal vertebrae of both the African species definitely preclude the assignment of our vertebra to an American *Dicraesaurus.* Since in general habitus and despite some rather striking differences, the vertebra comes closest to the *Camarosaurus* type, it is suggested provisionally to identify it as belonging to an animal of this genus and to name it *Camarosaurus annae.* By calling attention to its existence it is hoped that in the future additional skeletal parts more readily may be recognized, permitting a more complete description of the species and a more definite generic identification.

The vertebra was collected by the Carnegie Museum staff

during the excavations undertaken between 1909 and 1913 from the Jurassic Morrison formation in Dinosaur Quarry of Dinosaur National Monument, Utah. It was packed in Box 268 containing material from the locality B 56 on the quarry map published by Gilmore (plate 23).

The vertebra may be described as follows: The centrum of the pronouncedly opistocoelous dorsal vertebra is broader than high and inverse saddle-shaped with the ventral concavity extending up on both sides. There are no pleurocoels. The neural canal is small, round and slanting forward. The neural arch is very wide, flat both anteriorally and posteriorally and without the for *Sauropoda* typical laminae on both sides of the neural canal. The anterior zygapophyses are strikingly flat, broad and connecting at their bases by a thin horizontal lamina. The posterior zygapophyses are flat, broad and laterally projecting upward from a medial trough. The zygosphene has been restored and can not be described adequately in the present state. Above the zygapophyses rises a low, highly bifurcated spine with club-shaped rugose terminations. The transverse processes, proceeding immediately below the zygapophyses, are dorsally broad, flat and slightly slanting upward, terminating in rugose triangular-shaped facets. Ventrally they are flat and supported by vertical laminae which are single dorsally but ventrally bifurcate into two parts, the anterior joining with the style of the anterior zygapophyses, the posterior with the centrum. The capitular facets are placed low on the anterior part of the neural arch.

MEASUREMENTS

Total height of vertebra	444 mm.
Width of vertebra across transverse processes	775 mm.
Height of vertebral centrum	180 mm.
Width of vertebral centrum	230 mm.

The author wishes gratefully to acknowledge the many courtesies extended to him and his students by Dr. J. LeRoy Kay, Curator of Vertebrate Paleontology in the Carnegie Museum of Pittsburgh. Mr. T. Gmitter has

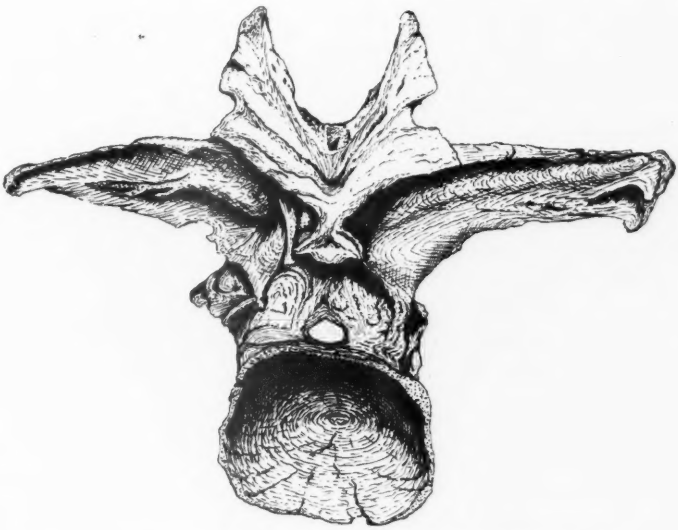

FIG. 1. *Camarosaurus annae*, n. sp. Dorsal vertebra, posterior view.

FIG. 2. *Camarosaurus annae*, n. sp. Dorsal vertebra, lateral view.

drawn the accompanying illustrations. The new species is named in honor of Miss Polly Ann Ratliff, of Natchez, Mississippi.

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